Drivers of regional and local boreal forest dynamics during the Holocene

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ACADEMIC DISSERTATION
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Abstract

Palaeoecological information provides means for understanding the processes behind past changes in forest composition, and offers valuable information on the potential impacts of predicted changes in climate on boreal vegetation. To fully understand the processes behind the long-term boreal forest dynamics both local and regional factors need to be considered.

In this work, the Holocene history of the western taiga forests, a continental variant of boreal forest characterized by the presence of Siberian larch (*Larix Sibirica*), in northern Europe is investigated using fossil pollen and stomata records from small forest hollow sites. The importance of the potential drivers of long-term boreal forest composition is quantitatively assessed using novel approaches in a palaeoecological context. The statistical method variation partitioning is employed to assess relative importance of climate, forest fires, local moisture conditions and human population size on long-term boreal forest dynamics at both regional (lake records) and local scales (small hollow records). Furthermore, wavelet coherence analysis is applied to examine the significance of individual forest fires on boreal forest composition.

The results demonstrate that Siberian larch and Norway spruce have been present in the region since the early Holocene. The expansion of spruce at 8000 – 7000 cal yr BP caused a notable change in forest structure towards dense spruce dominated forests, and appears to mark the onset of the migration of spruce into Fennoscandia. The mid-Holocene dominance of spruce and constant presence of Siberian larch suggests that taiga forest persisted throughout the Holocene at the study sites in eastern Russian Karelia.

Climate is the main driver of long-term vegetation changes at the regional scale. However, at the local scale the role of climate is smaller and the influence of local factors increases, suggesting that intrinsic site-specific factors have an important role in stand-scale dynamics in the boreal forest. When the whole 9000 year period is considered, forest fires explain relatively little of the variation in stand-scale boreal forest composition. However, this may be attributable to the variation partitioning method. Forest fires have a significant role in stand-scale forest dynamics when observed in shorter time intervals and the results from wavelet coherence analysis suggests that fires can have a significant effect on short-term changes in individual tree taxa as well as a longer profound effect on forest structure. The relative importance of human population size on variation in long-term boreal vegetation was statistically assessed for the first time using this type of human population size data and the results showing unexpectedly low importance of human population size as a driver of vegetation change may be biased because of the difference in spatial representativeness between the human population size data and the pollen-derived forest composition data.

Although the results strongly suggest that climate is the main driver of long-term boreal forest dynamics, the local disturbances, such as fires, species interactions and local site specific characteristics can dictate the importance of climate on stand-scale boreal forest dynamics.

Tiivistelmä

Paleoekologisen tiedon avulla on mahdollista ymmärtää paremmin metsän rakenteessa tapahtuneiden pitkäaikaisten muutosten taustalla vaikuttavia prosesseja. Tämä on tärkeää arvioitaessa todennäköisiä muutoksia, joita muuttuva ilmasto tulevaisuudessa aiheuttaa boreaalisissa havumetsissä. Pohjoiset havumetsät ovat monitahoisia ekosysteemejä ja ajallisten muutosten lisäksi on tärkeää ymmärtää metsän rakenteeseen vaikuttavien prosessien alueellinen mittakaava. Tämän vuoksi menneitä kasvillisuudessa tapahtuneita muutoksia ja niihin potentiaalisesti vaikuttaneita ympäristötekijöitä on tärkeä tarkastella sekä alueellisessa että paikallisessa mittakaavassa.

Tässä työssä tutkitaan läntisimpien taigametsien kehitystä viimeisten 10 000 vuoden eli holoseenin aikana. Taigametsiä luonnehtii Siperian lehtikuusen (*Larix Sibirica*) esiintyminen ja ne edustavat pohjoisten havumetsien mannermaista muotoa. Tutkimusalue sijaitsee Siperian lehtikuusen läntisimmällä luontaisella esiintymisalueella ja kasvillisuuden kehitystä tutkitaan pienistä metsäpainanteista saaduista fossiilisista siitepölyaineistoista ja havupuiden neulasten huulisoluaineistoista. Lisäksi työssä tutkitaan tilastollisin menetelmin eri ympäristötekijöiden merkitystä boreaalisessa kasvillisuudessa tapahtuneissa muutoksissa. Hajonnan ositus (variation partitioning) -menetelmän avulla selvitetään miten suuri suhteellinen merkitys ilmastolla, metsäpaloilla, paikallisilla kosteusolosuhteilla ja ihmispopulaation koolla on ollut boreaalisessa kasvillisuudessa tapahtuneissa muutoksissa sekä paikallisella (pienistä metsäpainanteista kerätty aineisto) että alueellisella (järvisedimenteistä kerätty aineisto) tasolla viimeisen 9000 vuoden aikana. Lisäksi metsäpalojen merkitystä metsän rakenteeseen määritetään tarkemmin aikasarja-analyysin (wavelet coherence) avulla.

Tulokset osoittavat, että Siperian lehtikuusi ja kuusi (*Picea abies*) ovat esiintyneet tutkimusalueella yhtäjaksoisesti jo viimeisten 10 000 vuoden ajan. Metsän rakenteessa on tapahtunut selkeä muutos 8000 – 7000 vuotta sitten, kun kuusen populaation huomattavan kasvun seurauksena mäntyjen, koivujen ja lehtikuusten luonnehtimat avoimemmat metsät muuttuivat tiheämmiksi kuusivaltaisiksi metsiksi. Tämä kuusen huomattava yleistyminen Luoteis-Venäjällä tukee aiempia tuloksia, jotka osoittavat kuusen leviämisen idästä Fennoskandian alueelle alkaneen noin 7 000 – 6 500 vuotta sitten. Siitepölyaineiston osoittama kuusen vallitsevuus puulajistossa keski-Holoseenin aikana ja lehtikuusen esiintyminen läpi holoseenin viittaavat siihen, että taigametsät ovat säilyneet tutkimusalueella koko holoseenin ajan, eikä alueella ole havaittavissa jalojen lehtipuiden yleistymistä holoseenin lämpökauden aikana kuten vain hiukan lännenpänä Fennoskandian alueella.

Tutkituista ympäristömuuttujista ilmasto on selkeästi merkittävin tekijä pitkän aikavälin muutoksissa boreaalisessa kasvillisuudessa alueellisessa mittakaavassa. Toisaalta paikallisessa mittakaavassa ilmaston rooli on selkeästi vähäisempi paikallisten tekijöiden merkityksen kasvaessa. Tämä viittaa siihen, että paikkaan sidotuilla tekijöillä on huomattava rooli metsän rakenteen muodostumisessa, kun muutoksia tarkastellaan paikallisessa metsäkuviotason mittakaavassa. Koko tutkimusajanjaksoa (9000 vuotta) tarkasteltaessa metsäpalot selittävät vain vähän metsärakenteessa tapahtuneista muutoksista, tämä voi kuitenkin olla seurausta käytetyn hajonnan ositus -menetelmän rajoituksista metsäpalo- ja siitepölyaineiston yhdistämisessä. Tulokset osoittavat, että metsäpaloilla on tärkeä rooli paikallisessa mittakaavassa boreaalisessa metsän rakenteessa tapahtuvissa lyhyen aikavälin

(< 1000 vuotta) muutoksissa. Aikasarja-analyysi osoittaa, että metsäpalot voivat olla merkittävä tekijä yksittäisten lajien lyhytaikaisissa muutoksissa, minkä lisäksi metsäpalojen seurauksena metsän rakenteessa voi tapahtua pidempiaikaisia perustavanlaatuisia muutoksia. Ihmispopulaation koon suhteellinen merkitys pitkän ajan kasvillisuuden muutoksissa osoittautui yllättävän vähäiseksi. On kuitenkin huomattavaa, että tässä työssä ihmispopulaation koon vaikutusta kasvillisuuden muutoksiin määritettiin tilastollisesti ensimmäistä kertaa käyttäen tämän tyyppistä radiohiiliajoitetuista arkeologisista löydöistä johdettua ihmispopulaation kokoa kuvastavaa aineistoa. Tämän vuoksi on mahdollista, että ihmispopulaation koon vähäinen suhteellinen merkitys kasvillisuuden muutoksissa on seurausta eroista ihmispopulaation kokoa kuvaavan aineiston ja kasvillisuutta kuvaavan siitepölyaineiston alueellisessa edustavuudessa.

Tutkimustulokset osoittavat, että vaikka ilmasto on merkittävin pohjoista havumetsäkasvillisuutta säätelevä tekijä, synnyttävät paikalliset tekijät, kuten metsäpalot ja paikalliset kasvupaikkaolosuhteet, alueellisia eroja boreaalisessa kasvillisuudessa tapahtuviin muutoksiin.

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Contents

Appendices: Publications I-III

List of original publications

This thesis is based on the following publications:

I Kuosmanen, N., Seppä, H., Reitalu, T., Alenius, T., Bradshaw, R.H.W., Clear J.L., Filimonova, L., Kuznetsov, O., Zaretskaya, N., 2015. Long-term forest composition and its drivers in taiga forest in NW Russia. Vegetation History and Archaeobotany DOI 10.1007/s00334-015-0542-y

II Kuosmanen, N., Fang, K., Bradshaw, R.H.W., Clear J.L., Seppä, H., 2014. Role of forest fires in Holocene stand-scale dynamics in the unmanaged taiga forest of northwestern Russia. The Holocene 24(11), 1503–1514

III Kuosmanen, N., Seppä, H., Alenius, T., Bradshaw, R.H.W., Clear J.L., Filimonova, L., Heikkilä, M., Renssen, H., Tallavaara, M., Reitalu, T., 2015. Importance of climate, forest fires and human population size in Holocene boreal forest dynamics in Northern Europe. (Submitted to Boreas)

The publications are referred to in the text by their roman numerals.

Authors´ contribution to the publications

N. Kuosmanen participated in the fieldwork for all four small forest hollow sites analyzed in this work and carried out the pollen, stomata, charcoal and peat humification analyses for three small hollow sites (papers I, II, III). The pollen and charcoal analyses for site Kukka Hollow were carried out by Jennifer Clear (papers I, III). For papers II and III N. Kuosmanen compiled a dataset containing original material from T. Alenius, R. Bradshaw, J. Clear, L. Filimonova, M. Heikkilä, K. Sarmaja-Korjonen, M. Tallavaara and H. Renssen.

I. The study was planned by N. Kuosmanen, H. Seppä and T. Reitalu. The statistical analyses were done by T. Reitalu. The results were jointly interpreted by N. Kuosmanen, H. Seppä and T. Reitalu. N. Kuosmanen was responsible for preparing the manuscript, while all authors commented and contributed.

II. The study was planned by N. Kuosmanen and H. Seppä. The statistical analyses were done by N. Kuosmanen and K. Fang. N. Kuosmanen and H. Seppä were responsible for preparing the manuscript, while all authors commented and contributed.

III. The study was planned by N. Kuosmanen and H. Seppä. The statistical analyses were done by N. Kuosmanen. The results were jointly interpreted by N. Kuosmanen and H. Seppä. N. Kuosmanen was responsible for preparing the manuscript, while all authors commented and contributed.

Abbreviations

AMS	Accelerator mass spectrometry
Cal yr BP	Calibrated radiocarbon years before present
ha	Hectare
HF	hydrofluoric acid
HTM	Holocene Thermal Maximum
KOH	Potassium hydroxide
LRA	Landscape Reconstruction Algorithm
LOVECLIM	Earth system model: LOch–Vecode–Ecbilt–CLio–agIsm Model
NaOH	Sodium hydroxide
NW	Northwestern
RDA	Redundancy analysis
summT	Mean summer temperature
wintT	Mean winter temperature
δ^{18}O_SAAR	Oxygen isotope record from Lake Saarikko

List of tables and figures

1 Introduction

1.1 Boreal forests in changing environmental conditions

Although located in northern latitudes with lower productivity, boreal forests have an important role in biodiversity offering a large variety of habitats for native species (Gauthier et al., 2015). The Boreal biome consists of 32 % of the world's forest cover and expands over a large circumpolar region in northern latitudes (Pan et al., 2011). Low winter and high summer temperatures together with low precipitation characterize the boreal ecosystem and its northern boundary is defined by the 10 – 13 °C July isotherm (Bonan and Shugart, 1989). Climatic conditions in the boreal region differ regionally and maritime climatic factors temper the boreal climate in western North America and Fennoscandia, while in Siberia and central Canada climate is colder and drier. Boreal forests are characterized by low species diversity and are dominated by few coniferous and deciduous tree species (Bonan and Shugart, 1998). Tree species composition differs regionally and in Fennoscandia the main forest forming tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), European aspen (*Populus tremula*), birches (*Betula* sp.), willows (*Salix* sp.) and alders (*Alnus* sp.), whereas larches (*Larix* sp.) are present in the taiga forests in Russia. In North American boreal forests, Black spruce (*Picea maritima*), White spruce (*Picea glauca*), and Jack pine (*Pinus banksiana*) are dominant species (Baldocchi et al., 2008). The Russian taiga forests cover approximately two thirds of the circumpolar boreal zone (Potapov et al., 2008) and the western range limit of Siberian larch (*Larix sibirica*), situated east of Lake Onega in NW Russia, is considered to mark the western boundary of the Russian taiga forest.

The boreal biome is projected to experience a rapid increase in temperature (Christensen et al., 2013) and predicting the ecological response of boreal forest to future climate changes is challenging (Jackson et al, 2009). The changing climate may alter abiotic (e.g. disturbances) and biotic (e.g. competition, insect outbreaks) drivers of boreal vegetation (Lindner et al., 2010; Scheffer et al., 2012) and these changes can have significant effect on diversity and the role of boreal forest as an important carbon stock (Lutz et al., 2013; Seidl et al., 2011; Thom and Seidl, 2015). Due to differences in forest composition between circumboreal regions, possible changes in climate may also affect these forests differently (Lindner et al., 2010). The water and energy exchange between boreal forests and the atmosphere play an important role in global climate dynamics, and changes in boreal vegetation composition can affect the climate. Therefore it is important to understand the process behind these changes in boreal forests.

Forest fires are considered as one of the most important disturbance factors regulating the age structure, species composition and succession dynamics of boreal forests (Kuuluvainen et al., 1998; Ryan, 2002; Kelly et al., 2013; Lehtonen & Kolström, 2000; Bradshaw et al., 2010). Projected climate change has been predicted to intensify the disturbance regimes in the boreal forests (Selikhovkin, 2005; Seidl et al., 2011, 2014) and increased fire frequency can influence boreal forest dynamics and their role in carbon storage (Carcaillet et al., 2002; Lindner et al., 2010; Seidl et al., 2014). The effect of forest fires on boreal forest dynamics is controlled by the fire regime, which includes such factors as fuel consumption, fire spread, intensity and severity of fire, seasonality and fire frequency (Bond & Keeley, 2005; Bowman et al., 2009; Conedera et al., 2009). Although climate is considered as the main controlling factor over fire regimes in boreal forests, under natural conditions the occurrence and spread of natural forest fires are controlled by complex interactions between climate, vegetation composition and structure, landscape variables and fire ignition (Higuera et al., 2009; Girardin et al., 2013: Marlon et al., 2013). Therefore the impact of fire on boreal forest composition also differs within the boreal region. European boreal forests include tree species that can resist fires, such as Scots pine, and fires in pine forests are mostly low intensity surface fires. In forests that are dominated by fire intolerant Norway spruce, fires can be severe and kill the spruce forest, but in these forests fire frequency is usually low (Wallenius et al., 2004; Ohlson et al., 2011 Rogers et al., 2015). In contrast, in North America the boreal forests are dominated by species that favor frequent fires, such as Black spruce, and fires have a more severe impact on boreal vegetation than in Europe (Rogers et al., 2015).

In addition to natural drivers, anthropogenic activity has influenced boreal forest dynamics. Before the advent of agriculture, the hunter-gatherers had local impact on the surrounding vegetation through burnings and favoring food-plants (Birks et al., 2014). Palynological and archaeological evidence demonstrates that the effect of Mesolithic hunter-gatherers can be locally detected even in northern Fennoscandia (Bergman et al., 2004; Hörnberg et al., 2005). A more apparent effect of human activity on boreal forests is connected to agriculture and farming practices. Slash-and-burn cultivation was widely used in Fennoscandia and it changed the natural fire regime and hence affected the structure of the boreal forests (Huttunen, 1980; Angelstam 1998; Granström and Niklasson, 2008; Wallenius et al., 2011). For example, burnings had a strong impact on boreal forests in Finland causing a compositional shift toward pine dominated forests, since the nutrient-rich spruce and deciduous forests were utilized for slash-and-burn cultivation (Heikinheimo 1915; Taavitsainen, 1987). During the 20th century, after cessation of the slash-and-burn cultivation, humans have mainly influenced the boreal forest composition through forest logging and related management strategies such as fire suppression (Halme et al., 2013).

Today boreal forests provide important ecosystem services and economic opportunities (Gauthier et al., 2015) and the majority of the boreal forests in Europe are extensively exploited. The last large unmanaged forested areas are found in remote and less accessible northern areas such as in the European Russian taiga (Yaroshenko et al., 2001; Potapov et al., 2008). Considered as the best preserved natural forest ecosystems in Europe, these taiga forests are crucial for understanding the natural long-term boreal forest dynamics in order to create successful management and conservation practices to maintain and restore the diversity of boreal forests (Angelstam et al., 1997; Kuuluvainen and Aakala, 2011).

1.2 Reconstructing regional and local scale boreal forest dynamics from sedimentary records

Sedimentary fossil records from natural archives such as lakes, peatlands and small forest hollows provide a valuable source of information on past changes in surrounding vegetation and environmental conditions. Reconstruction of past vegetation requires understanding of the spatial scale of the pollen deposited in the sediments in relation to the surrounding vegetation. The concept of source area of pollen has been widely addressed during the last decades. Jacobson and Bradshaw (1981) developed a simple qualitative model showing that pollen records from lake sediments reflect regional vegetation patterns, whereas pollen data from small forest hollows reflect the local vegetation around the site. During the last decades, the theoretical framework and quantitative models of pollen-vegetation relationships have been developed further. Prentice (1985, 1988) and Sugita (1993) presented the model of pollen representativeness on a lake surface (the 'Prentice-Sugita model'). Sugita (1994) developed this further and showed that there is a linear relationship between the size of the given site and the distance-weighted plant abundance of the surrounding vegetation represented in the pollen record. In small forest hollow sites (< 0.1 ha) a significant amount of the pollen originates less than few hundred meters from the coring site reflecting local vegetation around the site, whereas the pollen in larger sites (> 50 ha) can originate from tens of kilometers from the shore of the sampling site and can thus reflect regional vegetation dynamics (Jacobson and Bradshaw, 1981; Sugita 1993 2007a, 2007b).

The Holocene changes in regional vegetation patterns have been widely studied using lake records. However, the forest succession and the effects of stand-replacing disturbances, such as wind throws or forest fires, typically take place at the scale of a forest stand (Kuuluvainen, 2002; Shorohova et al., 2009). The past stand-scale forest dynamics can be successfully reconstructed from small forest hollows (e.g. Andersen, 1970; Bradshaw, 1988; Calcote, 1995; Davis et al. 1998; Parshall, 1999; Colpron-Tremblay & Lavoie, 2010; Sugita 2007; Overballe-Petersen and Bradshaw, 2011). Forest hollows are small (< 0.1 ha) depressions within a closed forest canopy and the pollen from these sites reflect vegetation within close proximity of the sites providing spatially high resolution data which is comparable to surveys of modern vegetation (Bradshaw, 2013). Furthermore, records from these small closed canopy sites reflect the local fire events and, compared to lake sediments, have less uncertainty about the source area of charcoal (Ohlson & Tryterud, 2000; Bradshaw et al., 2010). Therefore, records from these sites provide data for investigating the relationship between stand-scale changes in forest composition and local disturbances such as forest fires. In order to better understand the processes behind the past changes in boreal forest dynamics, both regional and local scale changes in long-term boreal forest composition and environmental conditions need to be considered.

1.3 Aims of this study

The long-term ecological dynamics of the Russian taiga forest have been previously studied (e.g. Syrjänen et al., 1994; Drobyshev et al., 2004; Shorohova et al., 2009; Aakala et al., 2011), but the Holocene paleoecology at the western margin of the Russian taiga forest, defined by the western range limit of Siberian larch, is less understood than that in the boreal forests in Fennoscandia. In this work, the general aim is to investigate the Holocene history of these western taiga forests in northern Europe and quantitatively assess the importance of the potential drivers of long-term boreal forest composition using novel approaches in palaeoecological studies. Though climate is considered as the main driver behind the range shifts of boreal tree species (e.g. Prentice 1998; Jackson and Overpeck, 2000; Soja et al., 2007; Bonan, 2008; Fisichelli et al., 2014), recent studies have highlighted that local processes mediate the effect of climate on vegetation composition at the sub-regional and local scale (Chapin et al., 2004; Kröel-Dulay et al., 2015). In this work, the relative importance of climate, forest fires, local moisture conditions and human population size on long-term boreal forest dynamics, at both regional and local scales, is quantitatively assessed utilizing the variation partitioning method (Borcard et al., 1992). To examine the significance of individual forest fires on boreal forest composition, wavelet coherence analysis (Grinsted et al., 2004) is employed. More specifically the aims of this thesis are as follows:

i) To investigate the Holocene history of the two keystone species, Siberian larch and Norway spruce, in the west ern range margin of the taiga forest in NW Russia, using fossil pollen and stomata records from small forest hollows (Papers I, II).

ii) To test the hypothesis that climate explains more of the variation in long-term boreal forest composition at the regional (lake records) than at the local (small hollow records) scale (Pa pers I, III).

iii) To examine the importance of forest fires in stand-scale boreal forest dynamics (Papers I, III) and assess the linkages between individual forest fires and boreal tree taxa (Paper II).

iv) To explore whether the human population size, derived from the frequency distribution of radiocarbon dated archaeological findings, can be applied as a potential driver of long-term boreal forest composition (Paper III).

2 Material and methods

2.1 Study area and sites

Four small forest hollow sites, analyzed for this work, are located at the ecological boundary between the boreal forest of Fennoscandia and the taiga forest in NW Russia (Fig. 1) (papers I, II, III). Geologically, the western part of the study area is part of Baltic shield with crystalline bedrock and the eastern part is located at the Russian (East European) Plain with predominantly calcareous bedrock (Gromtsev, 2002; Systra, 2003; Elina et al., 2010). The area was deglaciated 14 000 – 13 000 years ago (Svendsen et. al., 2004) and the landscape is characterized by undulating glacial topography. The climate becomes more continental towards the east, with a higher Gorczynski continentality index in the Russian taiga (35 – 40) than in Fennoscandia (30 – 35) (Gorczynski, 1922). The mean annual temperature is +3 °C, the coldest month is February with a mean temperature of -9 °C to -10.5 °C and the warmest month is July with a mean temperature of 16 – 17 °C (Nazarova, 2003). Biogeographically the study area is located in the middle taiga zone and the forests are characterized by Norway spruce, Scots pine, silver birch (*Betula pendula*), downy birch (*Betula pubescens*), aspen, grey alder (*Alnus incana*) and black alder (*Alnus glutinosa*). On the Russian plain (east of Lake Onega) Siberian larch, a more continental tree species, is growing in pine and spruce dominated forests and demonstrates the western range limit of the Russian taiga forest (Elina et al., 2010; Gromtsev, 2002). For paper III, the study area was expanded to cover an area spanning a west-east transect from Sweden (14°37’ E) to Finland and Russia (37°46’ E) located between 59° N and 63° N in the boreal forest zone and 17 sites (nine lakes and eight small hollows) were included in the study (Fig. 2 and paper III).

In order to trace the natural vegetation and fire history, four small forest hollows were selected from less populated, forested regions away from fields, villages or other visible forms of human activities. The study sites are small peat depressions within closed-canopy forest stands. To explore the Holocene history of Siberian larch at its western range margin, three sites were selected so that there are individual larches growing in the vicinity of the sites. Two of these sites, Larix Hollow (unofficial name) (N 61°50.755`, E 37°45.390`) and Mosquito Hollow (unofficial

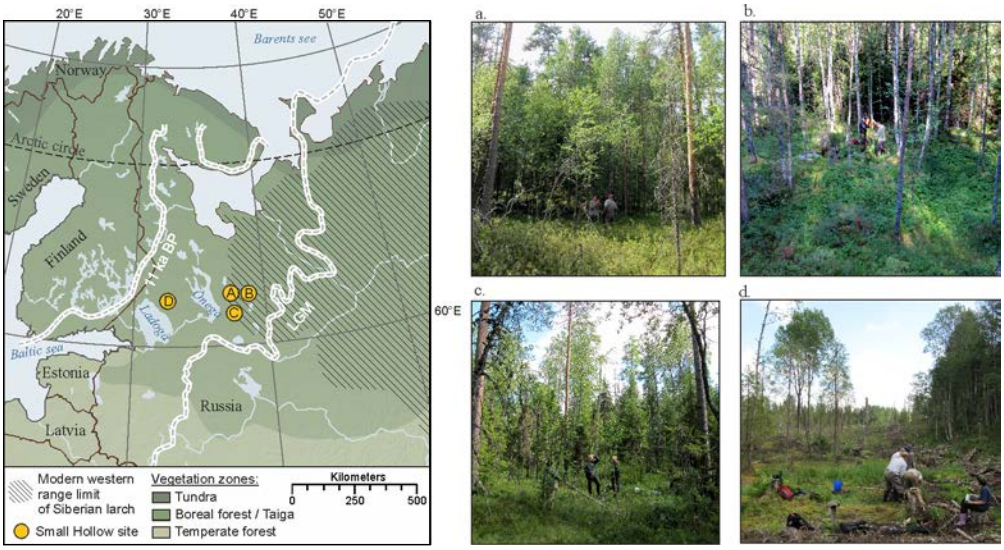

Figure 1. Map of the study area and small hollows analyzed in this study. a) Larix Hollow, b) Mosquito Hollow, c) Olga Hollow and d) Kukka Hollow. The locations of the sites are marked with yellow circles in the map. Distribution of *Larix sibirica* is based on modern distribution maps (Jalas and Suominen, 1973) and the extent of the ice sheet during the Last Glacial Maximum (LGM) and at 11 ka BP is based on Svendsen et al. (2004).

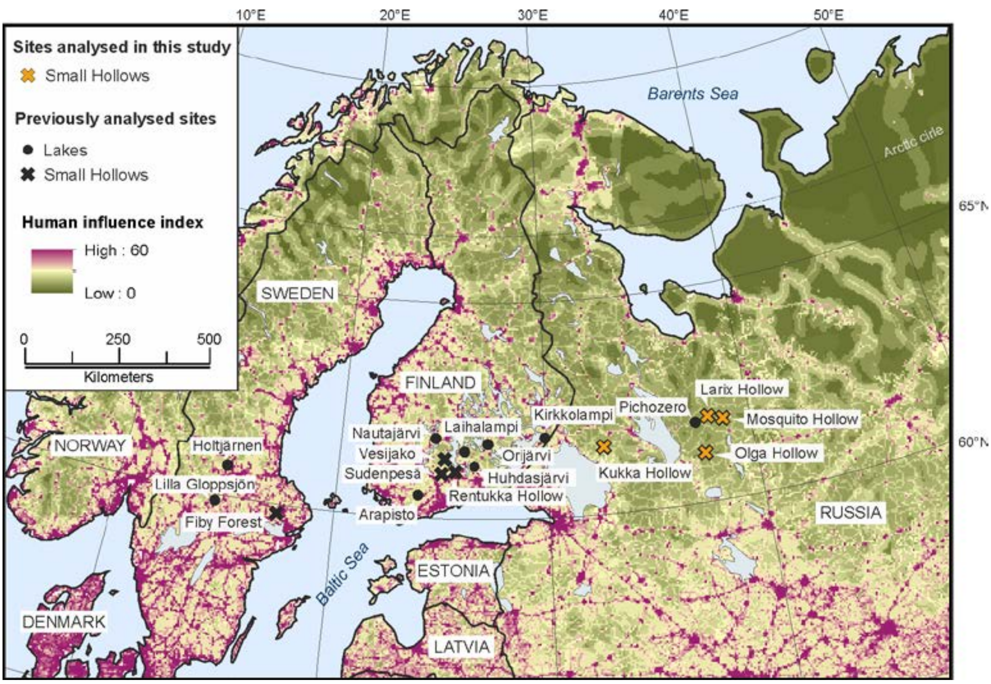

Figure 2. Map showing the location of the study sites used in this work. Small hollow sites analyzed in this work are shown as yellow crosses. Previously analyzed small hollow sites are expressed as black crosses and lake sites as black circles. Background map shows the present-day intensity of anthropogenic influence on the area derived from the human influence index (Wildlife Conservation Society –WCS and Center for International Earth Science Information Network – CIESIN 2005).

name) (N 61°51.112`, E 37°46.217`) are located in the Eastern Karelian region about 800 meters apart (Fig. 1). Both sites are surrounded by mixed forest, with spruce, birch, pine and larch as the main forest forming species (Fig. 1). The third site, Olga Hollow (unofficial name) (N 61°12.096`, E 37°35.430`), is located about 70 km south of Larix Hollow and Mosquito Hollow in the northern part of Vologda district (Fig. 1). Spruce is the dominant tree species surrounding Olga Hollow, with young trees and seedlings of larch. On the surrounding slopes of mineral soil, larch grows in a pine and spruce dominated forest. The fourth site, Kukka Hollow (unofficial name) (61° 38.957' 32° N, 45.174' E)(Fig. 1), is an elongated peat depression located in the Karelian district approximately 250 km west of the other three small hollow sites and outside the modern distribution range of Siberian larch. More detailed description of the sites is found in Table 1 and corresponding articles.

2.2 Sediment sampling and chronology

Sediment cores from the four small hollow sites were obtained with a Russian sediment corer (Jowsey 1966) in August 2010 and 2011. A 165-cm-long sediment core was extracted from Larix Hollow, a 200-cm-long core from Mosquito Hollow, a 226-cm-long core from Olga Hollow and a 616-cm-long core from Kukka Hollow. The cores were examined and photographed in the field for visible charcoal layers, transported to the laboratory at the University of Helsinki and stored at +4 °C for further analysis. Subsamples of 0.5 cm^3 were extracted for pollen, stomata and microscopic charcoal analyses at 1 cm intervals from Larix Hollow (159 samples in total), at 2 cm intervals from Olga Hollow (110 samples in total), at 8 cm intervals from Mosquito Hollow (26 samples in total) and from Kukka Hollow at 10 cm intervals for pollen (61 samples in total). Subsamples of 1 cm^3 were extracted for macroscopic charcoal analyses at 1 cm intervals (607 samples in total) from Kukka Hollow. Subsamples for the measurement of peat humification were extracted at 2 cm intervals from Larix and Olga Hollows and at 8 cm interval from Mosquito Hollow.

The chronology of the cores is based on AMS radiocarbon dating conducted by the Poznan Radiocarbon Laboratory, Poland and in the Laboratory of Chronology at the University of Helsinki, Finland. Terrestrial macrofossils and bulk samples of peat were used for dating and the dated levels of the cores were selected based on the changes in the pollen diagrams. Details of the dated samples can be found in table 1 and corresponding publications. All radiocarbon dates were calibrated using the IntCal09.14C calibration curve (Reimer et al., 2009) and the age-depth models for each site were constructed using the non-Bayesian Clam model package 2.1 (Blaauw, 2010) in the statistical software R (R Development Core Team 2015). The dates are expressed as calibrated years before present (cal yr BP).

2.3 Laboratory analyses

2.3.1 Fossil pollen and stomata data

All samples for pollen identification were prepared with standard procedures of KOH-, acetolysis- and HF-treatment (Fægri and Iversen, 1989). The samples were mounted in silicone oil and a minimum of 500 terrestrial pollen grains were identified using a 400x magnification. Pollen identification is based on Beug (2004), Moore et al. (1991), and a reference collection of the Department of Geosciences and Geography, University of Helsinki. In order to obtain more reliable information about the local presence of tree species during the Holocene, the fossil conifer stomata were identified from the pollen slides simultaneously with pollen identification. Sto-

Table 1. Description of small hollow sites analyzed in this study and related methods.

	Larix Hollow	**Mosquito Hollow**	**Olga Hollow**	**Kukka Hollow**
Coordinates	61°50` N, 37°45` E	61°51` N, 37°46`E	61°12` N, 37°35`E	61°38` N, 32°45`E
Size	< 0.1 ha	< 0.1 ha	< 0.1 ha	< 0.1 ha
Modern vegetation	Main tree species: Mixed forest with *Picea, Pinus, Betula* and *Larix sibirica* Ground layer: *Vaccinium myrtillus, Vaccinium uligonosum, Rhododendron tomentosum and Andromeda polifolia*	Main tree species: Mixed forest with *Picea, Pinus, Betula* and *Larix sibirica* Ground layer: *Vaccinium myrtillus, Vaccinium oxycoccus, Potentilla palustris, Menyanthes trifoliata, Carex* spp. and *Equisetum* spp.	Main tree species: Mixed forest with *Picea, Pinus, Betula* and *Larix sibirica* Ground layer: *Vaccinium oxycoccus, Andromeda polifolia, Rhododendron tomentosum, Potentilla palustris, Menyanthes trifoiata* and *Equisetum* spp.	Main tree species: Recently clear cut. Mixed forest with *Picea, Pinus* and *Betula* on surrounding slopes Ground layer: *Eriophorum angustifolium, Deschampsia cespitosa, Dryopteris carthusiana*
Chronology	Dated samples: six ^{14}C dates of peat samples and one ^{14}C date of terrestrial macrofossil Calibration: IntCal09 Age-depth model: non-Bayesian Clam model	Dated samples: three ^{14}C dates of peat samples and three ^{14}C dates of terrestrial macrofossils Calibration: IntCal09 Age-depth model: non-Bayesian Clam model	Dated samples: one ^{14}C date of peat sample, four ^{14}C dates of terrestrial macrofossils and two ^{14}C dates of gyttja Calibration: IntCal09 Age-depth model: non-Bayesian Clam model	Dated samples: nine ^{14}C dates of terrestrial macrofossil Calibration: IntCal09 Age-depth model: non-Bayesian Clam model
Sample analysis	- Pollen - Stomata - Microscopic charcoal - Peat humification Analysis	- Pollen - Stomata - Microscopic charcoal - Peat humification analysis	- Pollen - Stomata - Microscopic charcoal - Peat humification analysis	- Pollen - Stomata - Macroscopic charcoal
Statistical analyses	- Wavelet coherence - Variation partitioning - RDA	- Variation partitioning - RDA	- Wavelet coherence - Variation partitioning - RDA	- Variation partitioning - RDA
Paper	I, II, III	I, II, III	I, II, III	II, III

mata identification was based on the identification key by Sweeney (2004) and modern reference samples.

2.3.2 Sedimentary charcoal analyses

Microscopic charcoal analysis was conducted concurrently with pollen and stomata identification for Larix, Mosquito and Olga Hollows. In order to calculate the charcoal concentrations *Lycopodium* marker spores were added to the samples (Stockmarr, 1972). Opaque, sharp edged particles were identified as charcoal (Scott, 2010). The total amount of charcoal fragments was calculated from each slide and the concentration (particles/cm^3) of particles larger than 40 μm was used for the diagrams and the statistical analyses in this study. From Kukka hollow macroscopic charcoal analysis was conducted by Jennifer Clear in Liverpool. Subsamples were soaked in NaOH, sieved through 300 μm mesh and the residues were added to 80 ml of double distilled water. Charcoal particles >300 μm were counted on a petri dish using a grid base. Macroscopic charcoal concentrations are presented as total count of particles/cm^3.

2.3.3 Peat humification analyses

As an independent proxy for the local hydrological conditions, the degree of peat humification was analyzed from three small hollow sites (Larix, Mosquito and Olga Hollows) (paper I). Warmer and drier conditions are indicated by well composed peat layers, while less decomposed layers indicate cooler and wetter local conditions. The degree of peat humification was analyzed following the protocol defined by Chambers et al. (2010) based on the method of Aaby and Tauber (1975) and Blackford and Chambers (1993). Peat samples were soaked in NaOH and the amount of light transmitted through an extract was measured with a spectrophotometer (Lange DR 5000). The results are expressed as percentage (%) of light transmitted through the samples. See more detailed description of the method in paper I. Pollen, stomata, charcoal and peat humification data was plotted using C2 program (Juggins, 2003).

2.4 Climate data and human population size data

Climate data

Climate data was derived from LOVECLIM-climate model providing regional climate data at a monthly resolution. The model is an Earth system model of intermediate complexity and it includes atmosphere, ocean and sea ice, land surface and ice sheets and the carbon cycle (Renssen et al., 2009; Goosse et al., 2010). The climate variable used in the analysis includes three parameters; mean summer (summT) and winter (wintT) temperatures (papers I, III) and oxygen isotope (δ^{18}O_SAAR) (paper III). Mean summer (June – August) and winter (December – February) temperatures were calculated and the values expressed as difference from the pre-industrial (250 – 550 cal yr BP) mean. In order to have an independent palaeoclimatic variable for changes in summertime effective humidity, the oxygen isotope (δ^{18}O) record from Lake Saarikko in southern Finland (Heikkilä et al., 2010) was included in the analysis. The values reflect δ^{18}O composition of past lake water and are based on lake sediment cellulose (Heikkilä et al., 2010).

Human population size data

Two separate data sets were used for the human population size in paper III. For the prehistorical time period (9000 – 1000 cal yr BP) the human population size was derived from an archaeological data set (Tallavaara et al., 2010), which is assumed to reflect relative trends in the Holocene human population (Oinonen et al., 2010; Tallavaara et al., 2010). In paper III, the frequencies of calibrated median ages of radiocarbon dated archaeological findings were used to reconstruct the human population size. For the historical time period in Finland (1000 – 0 cal yr BP) the absolute human population data were derived from historical literature references (Huurre 1998; Virrankoski 2001; Meinander and Autio 2006; Tilastokeskus 2015).

2.5 Statistical analyses

Variation partitioning (Borcard et al., 1992) was used to investigate the relative importance of potential drivers on the variation in long-term boreal forest composition (Papers I, III). This method provides quantitative means to assess the relative importance of individual environmental variables in palaeoecological data (Reitalu et al., 2013). It allows the decomposition of the total variation in community data into components revealing the variation explained by independent variables, their joint effects and the fraction of the variation, which is unexplained by the known variables. In papers I and III long-term boreal forest composition reflected by pollen data was used as a response matrix. In paper I, three environmental variables; temperature (mean summT and wintT), forest fires (charcoal concentrations) and growing site wetness (degree of peat humification) were used as explanatory variables. In paper III, climate (mean summT and wintT and $\delta^{18}O$ isotope proxy for effective moisture), forest fires (charcoal concentrations) and human population proxy (frequency distribution of radiocarbon dated archaeological findings) were used as explanatory variables. Variation partitioning analyses were conducted using the Vegan package (Oksanen, 2011) in the statistical software R (R Development Core Team, 2015).

Ordination method redundancy analysis (RDA) (Legendre and Legendre, 1998) was employed to assess the quantitative relationship between long-term boreal forest composition and environmental variables (Paper III). The climate parameters (summT, wintT and $\delta^{18}O$_SAAR) forest fires (charc) and site variable were used as constraining variables. The pollen percentages of the most common pollen taxa present in all studied sites, reflecting the changes in long-term boreal forest composition, were used as the response variable. The significance of the marginal effects of a single constraining variable was assessed by ANOVA permutation test with (999 randomizations). RDA was conducted using the Vegan package (Oksanen, 2011) in the statistical software R (R Development Core Team, 2015).

Wavelet coherence application of wavelet analysis by Grinsted et al. (2004) was employed to examine the associations between forest fires and the four most common boreal tree taxa (*Picea, Pinus, Betula* and *Alnus*) (Paper II). Wavelet coherence analyses provides a novel approach to examine the relationship between past forest fires and vegetation composition (Cazelles et al., 2008; Torrence and Compo, 1998). The method can decompose the observations between two variables into the time-frequency profiles and measure the local correlation between the predictor and response variables in time frequency-windows. This allows the examination of the phase and strength of the effect of fires on tree taxa at different timescales. To test the statistical significance of the results, the Monte Carlo permutation methods are built into the analysis based on the red noise assumption with a first order autocorrelation. Wavelet coherence analyses were conducted in MATLAB with package by Grinsted et al., (2004).

3 Summary of original publications

3.1 Paper I

In paper I, the Holocene stand-scale vegetation dynamics were investigated based on pollen and stomata records. The main aim was to investigate the Holocene history of Norway spruce and Siberian larch in NW Russia. The second aim of the paper was to statistically assess the relative importance of the potential drivers of Holocene boreal composition by applying the variation partitioning method. For statistical analysis, the approximation of the Holocene boreal forest composition was derived from pollen data and pollen percentages of the ten most common pollen taxa (*Alnus, Betula, Corylus, Picea, Pinus, Ulmus, Salix,* Ericaceae, Cyperaceae, Poaceae) was used as the response matrix and temperature (mean summT and wintT), forest fires (charcoal) and growing site wetness (degree of peat humification) were used as explanatory variables. For the analysis, all data were averaged over 100-year intervals and analyses were carried out for four small hollows for the last 9000 years. In order to examine the relative importance of environmental variables through time, a moving window approach (Reitalu et al., 2013) was applied. The method provides information on the relative roles of the environmental variables over time by allowing the variation partitioning for subsets of data in different time windows. In addition, we examined the relative importance of climate, forest fires and growing site wetness separately on four most common tree taxa, namely spruce, pine, birch and alder. In this paper we also tested the hypothesis that temperature explains more variation in boreal forest dynamics at the regional scale rather than at the local scale by comparing the results from four small hollows (reflecting local vegetation) and two lakes (reflecting more regional vegetation).

The most conspicuous result is that pollen and stomata records clearly demonstrate the local presence of the two key taxa, Norway spruce and Siberian larch, at the western range limit of the Russian taiga since 10 000 cal yr BP. Spruce was widely present, but not dominant in the early Holocene in NW Russia. The expansion of spruce population at 8000 – 7000 cal yr BP significantly changed the forest structure, when the mixed pine-birch-larch forest declined and spruce became the dominant species. The spruce expansion in NW Russia occurs at the same time as the onset of the spruce migration westward into Fennoscandia.

Variation partitioning results indicate that temperature was the main driver of long-term changes in the Holocene vegetation composition in Russian taiga forests, whereas the role of local factors (forest fires and growing site wetness) was relatively low. However, when the analysis was conducted for shorter time periods, the data indicated a higher importance of forest fires. The relative importance of temperature in the variation in individual tree taxa varied between sites suggesting that the effect of temperature is connected to local characteristics of the site. The comparison between small hollows and lakes revealed that temperature explained larger proportion of the variation in regional forest composition. This is an expected result, as it is logical that the regional vegetation reflected by the pollen data from lakes in more in balance with changing climate than the local vegetation reflected by the small hollow data.

3.2 Paper II

Paper II focused on the Holocene fire history and the significance of forest fires in stand-scale dynamics in the unmanaged taiga forest in NW Russia. Fossil pollen, stomata and charcoal records were studied from three small hollows located in the western range limit of Siberian larch. Wavelet coherence method was applied to statistically assess the significance of forest fires on the vegetation composition at different time-scales. In the analysis, the phase and strength of the association between the four most common tree taxa (*Picea, Pinus, Betula* and *Alnus*) and forest fires were analyzed in a time-frequency window.

The results show remarkably different fire histories between the sites. In Larix Hollow the sedimentary charcoal layers corresponded with peaks in the microscopic charcoal concentration data and suggest frequent local fire events. However, in the data from Mosquito Hollow, located only 800 m apart from Larix Hollow, the absence of charcoal layers and the low charcoal concentrations suggest that site has acted as fire-free refugium throughout the Holocene. In Olga Hollow, the charcoal concentrations are generally low, but indicate increased fire activity between 7500 – 5500 cal yr BP. The differences in the fire histories between the sites located in a small geographical area demonstrate the importance of site-specific factors rather than climate as the driver of the local fire regime in the unmanaged taiga forests.

The wavelet coherence results demonstrate the significance of the forest fires in stand-scale forest dynamics. The impact of forest fires on vegetation varied from the short-term (< 200-year period) increase or decrease in individual tree taxa to the profound, longer-term (400 – 800 years or more) changes in vegetation composition. The clearest result is the strong negative association between spruce and local fire events, reflecting the fire-sensitivity of the spruce population. In contrast, birch and alder have strong positive associations with fires, which demonstrate their role as pioneer species that colonize the area after fire. Interestingly, pine had a neutral association with forest fires and the results suggest that the abundance of pine in our sites is connected to other factors, such as competition, rather than forest fires.

3.3 Paper III

In paper III, the importance of climate, forest fires and human population size on long-term regional and local boreal forest composition were addressed using variation partitioning. To test the hypothesis that climate explains more variation in long-term boreal forest composition at the regional scale compared to the local scale, pollen data from 17 sites (nine lakes and eight small hollows) spanning from Sweden across Finland to Russia were used to reconstruct the long-term vegetation composition. Climate, generated from LOVECLIM-climate model and $\delta^{18}O$ data, past forest fires as reflected by sedimentary charcoal data and human population size derived from the frequency variations in radiocarbon-dated archaeological findings, were used as drivers of Holocene boreal forest composition.

The results demonstrate that the climate clearly explains the highest proportion of the regional scale variation in boreal forest dynamics. However, this mostly concerns the regional vegetation and its importance at local scale is relatively small. Interestingly, the forest fires explain relatively low proportion of the variation in long-term boreal forest composition at both regional and local scale. The relative importance of human population size was assessed only using pollen data from lakes and the analyses were carried out separately for the prehistorical (9000 – 1000 cal yr BP) and historical (1000 cal yr BP to present) time periods. In general, the relative importance of human population size as a driver of changes in long-term forest composition is relatively low in both time-periods. However, since the human population size record is an average estimation for the whole study region, the low proportion of explained variation may be due to mismatch between the scales of the pollen data reflecting regional vegetation and the human population size data representing a much larger area.

4 Discussion

4.1 Holocene forest dynamics in taiga forest in NW Russia (papers I, II)

One of the most conspicuous results in this work is the constant presence of Siberian larch at its western range margin throughout the Holocene revealed by pollen and stomata records (Fig. 3). Though a small amount of larch pollen have been recorded in previous pollen diagrams from Eastern Russian Karelia (Devyatova, 1986; Demidov and Lavrova, 2001; Filimonova, 2006), the local presence of larch in the area has not been previously demonstrated by using stomata records or macrofossils. The stomata evidence is critical because larch is a notoriously silent species in palynological records, since its pollen is easily

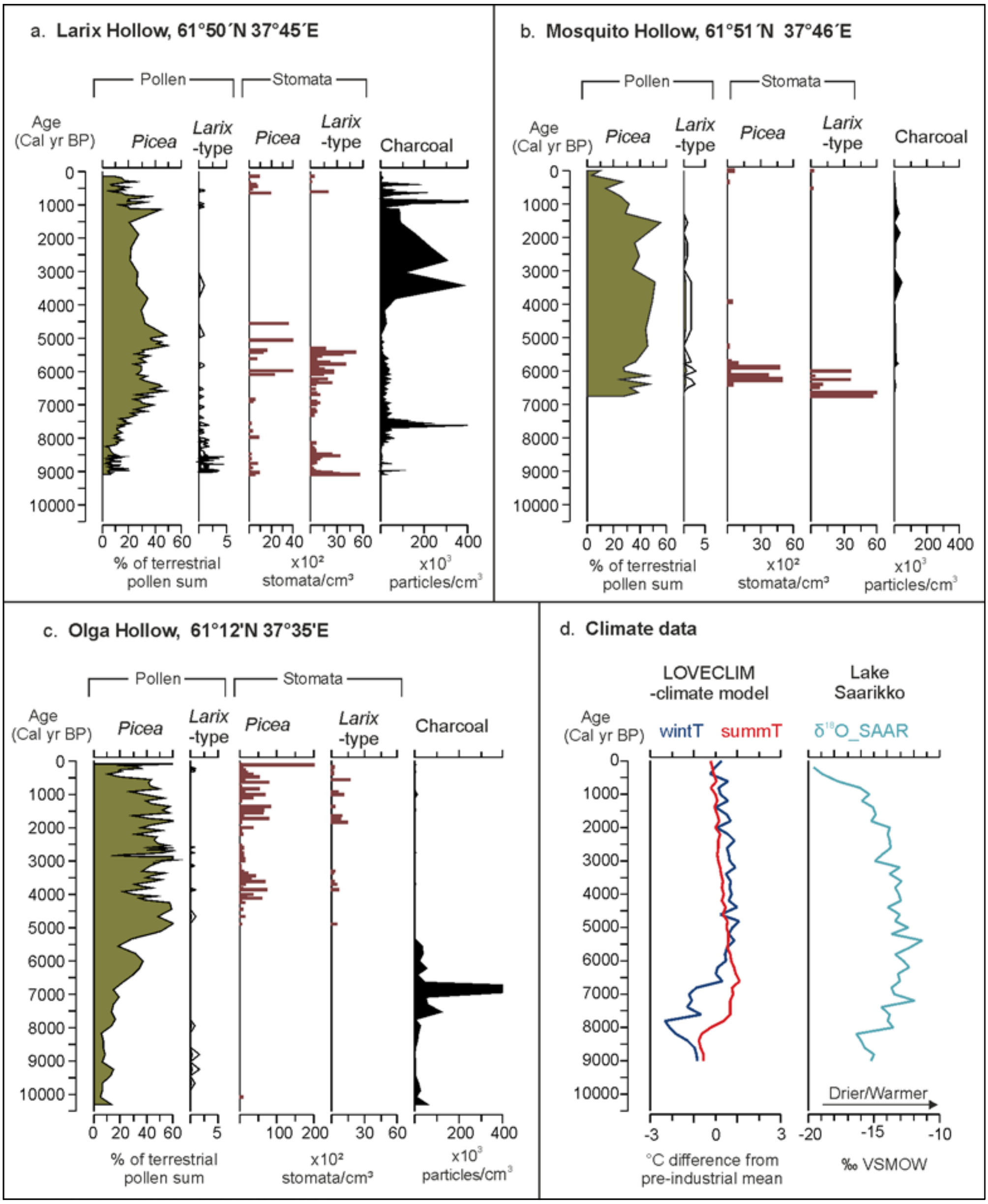

Figure 3. Diagrams showing the *Picea* and *Larix*-type pollen and stomata records from three small hollows from western range limit of Russian taiga a) Larix Hollow, b) Mosquito Hollow, and c) Olga Hollow. Pollen abundances are expressed as percentage of terrestrial pollen sum and shown with silhouette curves. Stomata concentrations (stomata/cm3) are shown with bars and charcoal concentrations (particles/cm3) with silhouette curves. d.) Climate data derived from LOVECLIM -climate model (Goosse et al., 2010) showing the mean winter (wintT) and summer (summT) temperatures in the study area and cellulose-inferred $\delta^{18}O$ record from Lake Saarikko in eastern Finland (Heikkilä et al., 2010).

broken and difficult to identify. Larch stomata are more abundant and easily identifiable, providing reliable evidence on local presence of the species at the study sites (Clayden et al., 1996). The previous studies from the study region have not included stomata analysis and therefore the presence of larch may have remained undetected. The early-Holocene presence of larch trees in the study area contradicts the previous hypothesis that, like spruce, the species would have migrated westwards during the Holocene (Binney et al., 2009). As discussed in paper I, larch is a continental species which can compete effectively with other tree species in harsh periglacial conditions, with cold winters and strong winds, due to its thick bark and deciduous leaves that offer protection against winter desiccation and wind abrasion (Gower and Richards, 1990; Kharuk et al., 2007). Therefore it is probable that during the late glacial, larch trees survived in periglacial conditions near the ice sheet margin and may have been more abundant in the light mixed *Pinus-Betula-Larix* forests that dominated the early Holocene landscape in the study area. Furthermore, Kullman (1998) and Öberg and Kullman (2011) reported the potential presence of larch in the Scandes mountains during the early Holocene.

However, presently larch grows in scattered populations in spruce and pine dominated forests in its western range margin. The reason why larch stayed in its western range margin for the last 10 000 cal yr BP, but has not migrated westward can only be speculated. Like larch, spruce favors nutrient rich habitats, but unlike larch it is a shade tolerant species (Gower and Richards, 1990). Since these two species have partly overlapping ecological niches, it is probable that the change towards a warmer climate favored spruce at the expense of more continental larch. This is corroborated by the studies from Siberian larch dominated forest from Siberia indicating ongoing greening with dark conifers, such as spruce, overtaking the light larch dominated forests (Kharuk et al., 2007; Shuman et al., 2011).

An equally important feature in our pollen and stomata records is the widespread presence of spruce in Russian Karelia from 10 500 cal yr BP onwards. This together with other studies (Subetto et al., 2002; Wohlfarth et al., 2002, 2004, 2007; Elina et. al., 2010) in the surrounding areas in Karelian Isthmus and eastern Russian Karelia suggest that spruce was widespread, but not dominant in the late-glacial and early Holocene forest vegetation.

The expansion of spruce population at 8000 – 7000 cal yr BP initiated significant change in forest structure (Fig. 3), when the light *Pinus-Betula-Larix* forest was replaced by denser spruce dominated coniferous forest and spruce remained as the dominant tree species until the late Holocene. This together with the constant Holocene presence of Siberian larch suggests that taiga forests were growing in the region throughout the Holocene. No notable increase in temperate tree species in forest composition occurred during the Holocene Thermal Maximum (HTM) in the region. These results differ from the clear northward range shift of temperate tree species, such as *Corylus, Tilia*, and *Quercus* in Fennoscandia (e.g. Heikkilä and Seppä, 2003; Alenius and Laakso, 2006; Miller et al., 2008; Seppä et al., 2015) during the HTM between 8000 – 4000 cal yr BP (Heikkilä and Seppä 2003; Seppä et al., 2009a). This may be attributable to more continental climate setting with low winter temperatures in the region, since the lower tolerance of temperate deciduous trees to the extremely low winter temperatures, which can occur in more continental parts of Europe, may have favored coniferous tree taxa (Miller et al., 2008).

The rise to dominance of spruce is roughly synchronous at all studied sites in Russian Karelia (in paper I, figure 4) and roughly concomi-

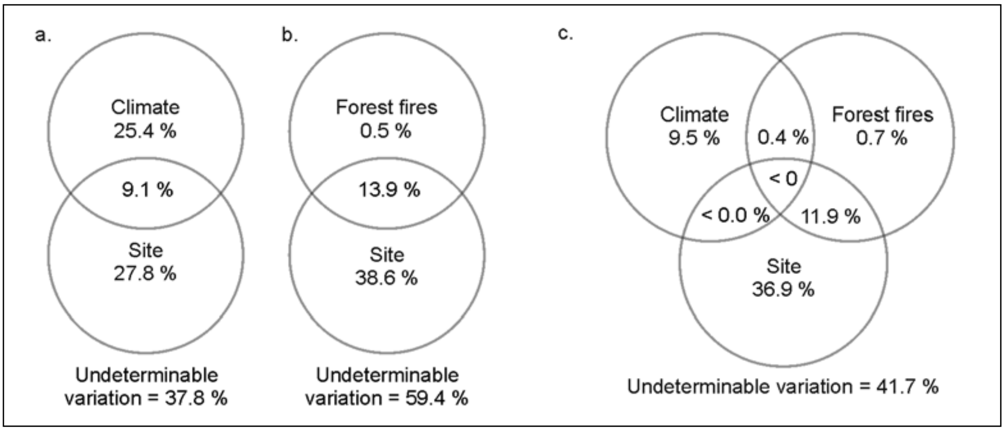

Figure 4. Variation partitioning results for the whole 9000 year study period. a) In pollen data from all lakes pooled together in terms of fractions of variation explained by climate and site variables, b) In pollen data from all lakes with charcoal record pooled together in terms of fraction of variation explained by forest fires and site variables, c) Variation partitioning results for the last 9000 cal yr BP in all small hollows pooled together in terms of fractions of variation explained by climate, forest fires and site variables.

tant with the well-established westward spread of spruce to Fennoscandia starting in eastern Finland at 7000 – 6500 cal yr BP (e.g. Tallantire 1972; Giesecke and Bennet, 2004; Latalowa and van der Knaap, 2006; Seppä et al., 2009b). Therefore, the widespread expansion of spruce population seems to mark the beginning of the westward migration of spruce to Fennoscandia that is traditionally connected to the change in climate towards more cool and moist conditions (Miller et al., 2008; Seppä et al., 2009b). However, the spruce expansion in Russian Karelia coincides with the onset of the HTM at 8000 cal yr BP. As discussed in paper I, it is possible that the prevailing climatic conditions with lower-than-present winter temperatures and warmer summers with longer growing season favored spruce that may have outcompeted other tree taxa. In addition, the oxygen isotope records indicate short-term increase in moisture little before 8000 cal yr BP (Fig. 3). This may have been a facilitator for the expansion of spruce. Similar response have been recorded by (Borisova et al., 2011) from western Siberia, where change from light larch dominated forest to dark spruce dominated coniferous forests was attributed to changes in moisture conditions.

During the late Holocene, pollen records from four small hollows show decline in *Picea* pollen curve from 2000 cal yr BP to present (see paper I, figure 4). Similar trend in the Holocene history of the species have been recorded in small hollow and lake records in Fennoscandia and Baltic countries. In general, spruce decline has been connected to increased human induced fires and especially to slash-and-burn cultivation practices (e.g. Alenius et al., 2008; Heikkilä and Seppä, 2010; Niinemets and Saarse, 2006; Pitkänen et al., 2002). However, as the fire histories from the small hollow sites in eastern Russian Karelia demonstrate (Fig. 3) the concurrent spruce decline in each site during the last two millennia cannot be explained by increased fire activity. This suggests that the spruce decline is a large scale phenomenon in northern Europe, probably initiated by the changes towards less continental climate conditions during the Late Holocene.

4.2 Climate drives the long-term boreal forest dynamics at regional scale (Papers I, III)

The Holocene range shifts of tree taxa in connection to changing climate in Europe is well recognized (e.g. Birks, 1986; Prentice et al., 1998; Soja et al., 2007; Miller et al., 2008; Giesecke et al., 2011; Hickler et al., 2012) and corroborated by the results of papers I and III demonstrating that climate is the main driver of the regional long-term boreal forest dynamics. In general, temperature and moisture conditions are considered as the main limiting factors for the growth of boreal tree taxa (Bonan and Shugart, 1989; Woodward, 2004) and as our climate variable was comprised of mean summer and winter temperatures and the affective humidity, the results were expected. Noteworthy is the high amount of variation explained by site factor (Fig. 4) and that a substantial amount of variation was left unexplained. This demonstrates the importance of differences in vegetation composition, succession stage and the disturbance regimes that may govern the impact of climate on long-term changes in boreal forest dynamics in different regions (Lindner et al., 2010). However, the forest fires explain individually, very little of the regional scale variation, which probably is attributable to the local nature of fires.

4.3 Drivers of stand-scale boreal forest dynamics (Papers I, II, III)

Although climate explains the highest amount of the variation also at local scale, its importance is clearly less prominent than at the regional scale. The high amount of variation explained by the site factor and the fact that almost half of the variation is left unexplained (Fig. 4c) demonstrates the complexity of the processes behind the long-term stand-scale boreal forest dynamics. It is important to note that in addition to the factors included to the analysis in this work, the stand-scale boreal forest dynamics may be at-

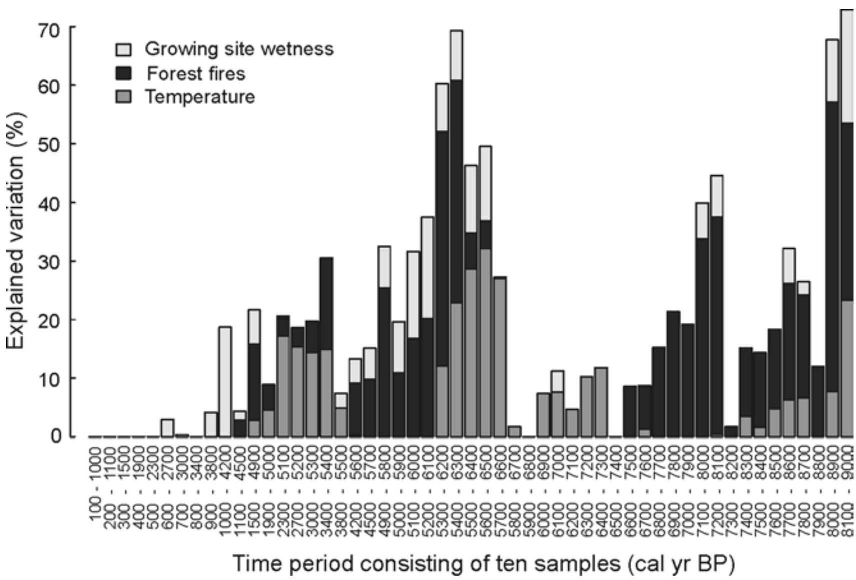

Figure 5. Results for variation partitioning for ten most common pollen taxa (*Alnus, Betula, Corylus, Picea, Pinus, Ulmus, Salix*, Ericaceae, Cyperaceae, Poaceae) from Larix Hollow in terms of fraction of the variation explained by temperature, forest fires and growing site wetness. The variation partitioning has been carried out in the subset of ten successive pollen samples.

tributable to several other factors, such as soil characteristics (Bonan and Shugart, 1989; Kolb and Diekmann, 2004; Kunes et al., 2011), light availability (Diekmann 1996; Miller et al., 2008), natural disturbances such as wind throws and insect outbreaks (Peterken, 1996; Selikhovin, 2005; Hof and Svahlin, 2015) and interspecific competition (Mitchell et al., 2006; Seppä et al., 2009b; Post, 2013; Zhang et al., 2015). The significance of the factors not included in this work is also evident from the results of moving window approach that show the relative importance of used environmental variables on boreal vegetation composition through time in subsets of ten samples reflecting shorter time periods (varying in length due to the uneven sedimentation rate) (Fig. 5). The variation explained by climate, forest fires and growing site wetness varies notably and rarely exceeds over half of the explained variation. Therefore, it can be assumed that the changes in stand-scale boreal composition are also attributable to several other factors, which were not possible to include in this work.

Senici et al. (2013) demonstrated the significance of local moisture conditions on fire regime and hence to the local vegetation. In paper III, the peat humification data were employed as a proxy for changes in local moisture conditions in order to detect the relative importance of local hydorogical conditions on stand-scale forest dynamics. The degree of peat humification has been used as palaeoclimatic proxy indicating especially the shift in moisture conditions (e.g. Blackford, 2000; Borgmark, 2005; Chambers et al., 2012). However, the peat-forming ecosystem is sensitive to the changes in local vegetation (Yeloff and Mauquoy, 2006) and disturbances, such as forest fires, may affect water-table level. Thus, the local microclimatic conditions interpreted from peat humification data may be biased and needs to be considered with caution. However, there are several studies suggesting that there may have been substantial changes in the groundwater level and associated trends in paludification in Fennoscandia (e.g. Almquist-Jacobson, 1994; Hammarlund et al., 2003; Väliranta et al., 2007; Weckström et al., 2010; Edvardsson et al., 2012). Therefore, it is evident that in future studies the local hydrological conditions need to be included as one of the potential driver of stand-scale forest dynamics.

Both local factors, forest fires (papers I, II, III) and local moisture conditions (paper I), explain a relatively low amount of variation in stand-scale boreal forest dynamics (paper I) when the whole 9000 year study period was included in the analysis. However, especially the importance of fires increase when the shorter time intervals (consisting of subsets of ten samples) are observed (Fig. 5 and see paper I). Although the low importance of local factors in long-term boreal forest composition may be an artefact created by the variation partitioning method (see chapter 4.5), these results suggest that when investigating the drivers of local boreal forest dynamics, the consideration of temporal scale is necessary.

4.3.1 Importance of fire on stand-scale boreal forest dynamics (Papers I, II, III)

Since fire is considered as one of the key factors maintaining the mosaic age structure and patchy composition characteristic to natural boreal forests (e.g. Zackrisson, 1977; Hörngberg et al., 1995; Kuuluvainen and Aakala, 2011; Drobyshev et al., 2014), the relative importance of forest fires in the variation of long-term boreal stand-scale dynamics was unexpectedly low (Fig. 4). It is probable that this result is biased and attributed to the variation partitioning analysis method used in this study (see chapter 4.5). However, in boreal forests the lifespan of dominant tree species may be equal or even longer than the fire intervals (Josefsson et al., 2010), which may hold back the effect of fire on vegetation dynamics. Fur-

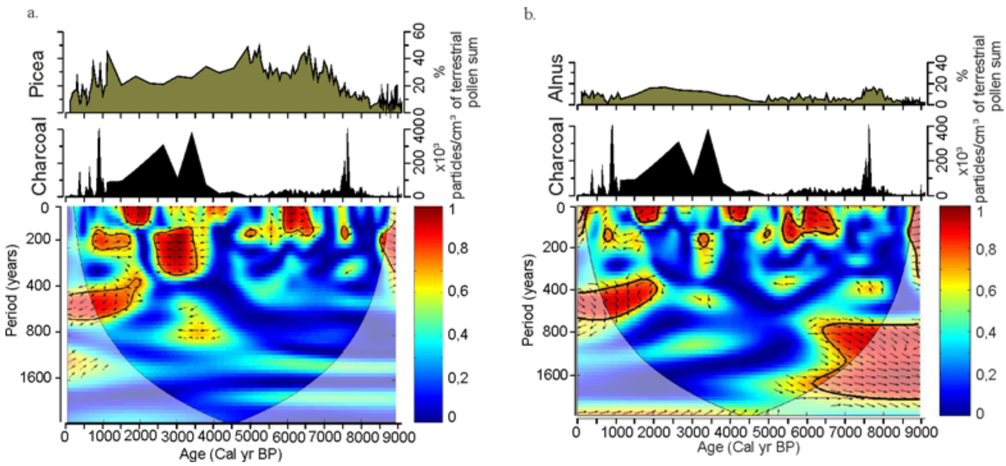

Figure 6. Wavelet coherence results from Larix Hollow of *Picea* pollen and charcoal concentrations (a) and between *Alnus* pollen and charcoal concentrations (b). Pollen curve (% of terrestrial pollen sum) and charcoal concentrations (particles/cm³) are shown on top of the wavelet output figure. The wavelet figure shows the correlation between two fluctuating time series (charcoal concentration and pollen values). Age (cal yr BP) is shown on the x-axis and the time period (year) on y-axis. The color bar expresses the strength of correlation, where shades of red mean strong and shades of blue weak correlation. Arrows pointing to the left indicate an anti-phase fluctuations expressing negative correlation and arrows pointing to the right indicate an in-phase fluctuations showing positive correlation. Black contour lines indicate regions in which the observed wavelet coherence values are statistically significant based on Monte Carlo calculations.

thermore, Scots pine can resist fires and though the fires are usually frequent in pine dominated sites they do not necessarily cause fatal damage to the trees (Zackrisson, 1977).

Although the results suggest low importance of fires in the long-term perspective, the significant role of fires on short-term stand-scale boreal forest dynamics is demonstrated when the variation partitioning analysis is performed in shorter time intervals in moving window approach (Fig. 5). Furthermore, the results of wavelet coherence analysis do not only demonstrate the significant role of fires in the changes of individual species in short-term (<200 year period), but indicate longer (>400 – 800 year period) profound changes in stand-scale forest composition (Fig. 6). For example, it is probable that in Larix and Olga Hollows the period of high-intensity fires at 7500 – 7000 cal yr BP has destroyed the extant forest type and top soil and thus created openings for spruce invasion and facilitated a shift towards spruce dominated closed forest (Fig. 3). Thus, it can be assumed that change in fire frequency is an important driver of the changes in stand-scale forest composition. However, the local vegetation composition and the severity of fires may regulate the impact of fires (Ryan, 2002). The significance of fires in stand-scale succession dynamics in short intervals is demonstrated by the species specific wavelet analysis indicating strong short-term (≤ 200 year period) association with all four analyzed tree taxa and forest fires (Paper II). The results clearly demonstrate the strong positive short-term effect of fires on birch and alder suggesting that fire has initiated the succession of these pioneer species throughout the Holocene. The strong negative association between spruce and forest fires is coherent with the known fact that spruce is a fire intolerant species (Heikinheimo 1915, Zackrisson, 1977). Considering that spruce has been present at the sites from the early Holocene and that the maximum values of *Picea* pollen correspond with periods of low fire frequency in all studied sites

(Fig. 3), it seems that fires have an important role in the changes of spruce population in the unmanaged taiga forest, at least at local scale in the region of a strong continental climate.

4.4 Human population size as potential driver of Holocene boreal forest dynamics (Paper III)

Traditionally the pollen data have been used to track the past human influence on vegetation (Behre, 1988) and especially the onset of cultivation practices (e.g. Rankama and Vuorela, 1988: Taavitsainen et al., 1998; Alenius and Laakso, 2006). However, in this work the applicability of human population size proxy, derived from the frequency of radiocarbon dated archaeological findings, as one potential driver of the long-term regional boreal forest dynamics was statistically assessed for the first time. Previously Reitalu et al. (2013) made an effort to assess the relative importance of human activity in boreonemoral vegetation in Estonia during the last 5000 years based on palynological records. Their results displayed a higher impact of human activity compared with the results obtained in this work that demonstrates relatively low importance of the human population size on long-term changes in boreal forest composition during the Holocene. Especially the importance of human population size during the historical time period was unexpectedly low in general (paper III, figure 6). The differences between the results presented in this work and Reitalu et al. (2013) may be partly attributable to the earlier onset of cultivation in Estonia than in Fennoscandia (Poska et al., 2004). However, there are also notable difference between the analysis used by Reitalu et al. (2013) and the method applied in this study. Reitalu et al. (2013) reconstructed the human impact variable from the sedimentary fossil pollen and charcoal records as one parameter of the human impact variable, whereas in this study the human population size proxy were independent from the fossil record. The advantage of using sedimentary fossil records is that they provide a more local signal of human activity than the data reconstructed from a regional data set of archaeological findings. However, the human impact variable reconstructed from the same pollen data from which the forest composition is reconstructed creates a danger of circularity. The advantage of our analysis is the independence of the human population size proxy from the pollen records that are used to reconstruct the long-term forest composition. Therefore, it offers a unique opportunity to assess the relative importance of human population size on the changes in Holocene boreal forest composition in Finland.

The method of using the frequency of radiocarbon dated archaeological findings to reconstruct the human population size is widely applied (e.g. Gamble et al., 2005; Shennan and Edinborough, 2007; Tallavaara et al., 2010). However, the variation in calibration methods of radiocarbon dates and sample size may hamper the detection of the correct short-term variation in human population size (Williams, 2012; Shennan et al., 2013). Moreover, the older sites may be underrepresented due to the time-dependent taphonomic loss of archaeological sites (Surovell and Brantingham, 2007; Surovell et al., 2009; Williams, 2012). Most importantly, the estimate of the prehistoric human population size is an average value for southern and central Finland, and the historical population estimate is for whole of Finland. Hence, it is likely that these values do not reliably reflect the changes in human population size around the individual lakes from where pollen data for reconstructing the forest composition were derived. Since this was the first time that the importance of this type of human population size data on long-term boreal forest composition was statistically assessed, and considering the possible source of bias in the analysis, the results (presented and discussed in more detailed in paper III) demonstrating the unexpectedly low individual effect of human population size on the long-term boreal forest dynamics must be considered with particular caution.

4.5 Assessment of the methods and data

The variation partitioning method is commonly applied in ecological studies. However, in the context of paleoecology the method has been less utilized. Reitalu et al. (2013) showed the potential of variation partitioning in assessing the relative importance of past environmental variables on the variation in past vegetation composition. In this work, the variation partitioning method was employed in papers I and III, and the results for the entire 9000 year study period gives ground to discuss the usefulness of this method to assess the importance of abrupt and short-term local environmental factors on changes in vegetation in long-term perspective. It can be assumed that the method detects the connection between the overall trends in Holocene climate and regional vegetation patterns rather reliably and the results regarding the importance of climate on the long-term changes in vegetation can be considered trustworthy. However, since the wavelet coherence analysis suggests the significant role of fires in both the short-term and longer time-perspective, and the RDA results show the significance of fires also in long-term forest dynamics at the local scale, it is probable that the variation partitioning results showing the unexpectedly low relative importance of fires on the variation in long-term stand-scale forest composition might be biased. It is important to note that variation partitioning analysis considers the entire time period included in the analysis and the method records the overall trend, but not the direction of the change. Therefore, the short-term positive associations between the stand-scale vegetation and environmental variable at one point may be cancelled with negative association in another point of time. Therefore the impact of the short-term changes in fire frequency and in the local moisture conditions on changes in long-term stand-scale forest dynamics may remain low or unidentified. Thus, the results of this work suggest that employing the variation partitioning method to assess the connection between past vegetation and local environmental conditions needs to be carefully considered.

The wavelet coherence analysis was proven to be a useful method for examining the association between forest fires and boreal tree taxa. Whereas the variation partitioning method only records the overall relative importance, wavelet coherence also reveals the phase and the strength of the association providing more comprehensive information of the relationship between the two variables. Moreover, the post-fire plant succession may take place over tens of years (Lampainen et al., 2004; Angelstam and Kuuluvainen, 2004; Shorohova et al., 2009) and the peak in charcoal record might not match with the corresponding change in pollen record. Such a time-lag may remain undetected when using the variation partitioning, however wavelet coherence analyses observes the change of two variables in moving time frequency window and therefore can better spot the correlation between two variables. In future, more flexible techniques based on for example, Bayesian approaches (Toivonen et al., 2001; Holmström and Erästö, 2002) could be used to better detect the long-term importance of fires or other short-term events on stand-scale forest dynamics.

It is also important to note that in this work the temperature data was derived only from one climate model and it would be beneficial to test if the results would differ depending on the applied climate model. However, the LOVECLIM-climate model was chosen for this study, because it is a regional climate model that provides better temporal resolution compared to other available models. Furthermore, the derived temperatures correspond with changes in independent $\delta^{18}O$ record (Fig. 3) and with the climate reconstructions for northern Europe (e.g. Heikkilä and Seppä, 2003; Seppä et al., 2009a). In addition, as discussed in paper III, the charcoal data might be biased since for example in lake sediments the prolonged charcoal accumulation after fire may cause a 'false positive' signal in the records, whereas in small hollows the fine-scale patterns of the fire may result in too conservative estimates of fire frequency, when the fire may not advance over the whole surface of the site (Pitkänen et al., 2003; Higuera et al., 2005).

4.6 Implications for future research

The constant Holocene presence of Siberian larch at its modern western range limit, presented in this work, together with studies of Kullman (1998, 2008) and Öberg and Kullman (2011) suggesting the early Holocene presence of the species in the Scandes mountains, evokes the question of the late glacial – early Holocene distribution of the species. When and where larch migrated to its modern western range limit? Answering these questions would require temporally longer records from a wider area east of the present western distribution limit of the species. To detect the possible early Holocene presence of larch in southern Fennoscandia, small hollows along a transect from the modern western range limit of the species across Russian Karelia to southeastern Finland should be sampled. Also in future studies the stomata records should be employed in order to detect the local presence of Siberian larch.

The changes in long-term boreal forest composition, reflected by pollen data, in relation to Holocene changes in climate in the Russian taiga, show different pattern compared to the changes in the Fennoscandian boreal forest. The next step towards a more comprehensive understanding of these taiga forests could be the reconstruction of the actual vegetation cover in the region during the Holocene. In recent years, the methodological advances in quantitative reconstructions of past vegetation from fossil pollen data have led to development of quantitative REVEALS- and LOVE-models (Sugita 2007a, 2007b; Sugita et al., 2010), which have been successfully used in reconstructing the Holocene land cover (e.g. Gaillard et al., 2008; Mazier et al., 2012; Nielsen et al., 2012; Marquer et al., 2014). While the reconstruction of past vegetation has previously reflected the changes in pollen percentages or concentrations, these new models provide means to reconstruct the actual vegetation cover and reveal the actual proportion of certain species of the vegetation composition. Applying these approaches could increase the knowledge of the Holocene dynamics in the Russian taiga forests. However, these models require a higher number of large lake and small forest hollow sites as well as information of the pollen productivity of tree species, which is depended on the forest type and regional habitat characteristics (Baker et al., 2015). Currently there are no pollen productivity estimates of Siberian larch in taiga forests, which would be crucial in reconstructing the actual vegetation cover in European Russian taiga forests.

This work also confirms the assumption of the connection between regional climate setting and vegetation patterns, often intuitively assumed in palaeoecological studies and used as grounds for the species distribution modelling or to reconstruct past climates. Species distribution models that are used to reconstruct and predict the past and future changes in species distribution are based on climate data and results of this work imply that these models are relevant only for regional-scale vegetation patterns. The stand-scale changes in vegetation are influenced by a complex set of local factors and hence probably too intricate to be modelled by presently available modelling approaches. The pollen data from lake sediments have been used in paleoclimate reconstructions to reconstruct past temperatures (e.g. Huntley et al., 1989; Seppä and Birks, 2001; Bartlein et al., 2011). These reconstructions are based on pollen-climate calibration models that assume that pollen composition is related to regional climate (Seppä et al., 2004; Salonen et al., 2012). Results from this work demonstrate the high importance of climate on the variation in pollen data from lake records, hence confirming the usability of these sites for paleoclimate reconstruction, whereas the pollen data obtained from small hollows reflect the local vegetation pattern and are not appropriate for paleoclimate reconstructions.

5 Conclusions

In this work, fossil pollen, stomata and charcoal records were used to enhance knowledge of the Holocene history of unmanaged taiga forest in a lesser studied area of NW Russia. In addition, the importance of the potential drivers of long-term boreal forest dynamics were statistically assessed with variation partitioning and wavelet coherence methods that are novel approaches in palaeocological context. The main findings of this study can be summarized as follows:

i) Pollen and stomata records from small hollow sites demonstrate that Siberian larch and Norway spruce have been present in the study region since the early Holocene. The expansion of spruce population at 8000 – 7000 cal yr BP caused notable change in forest structure, when the light pine-birch-larch forest was replaced by dense spruce dominated forests. Moreover, the spruce expansion seems to mark the onset of the migration of spruce towards Fennoscandia. The mid-Holocene dominance of spruce and constant presence of Siberian larch suggests that taiga forest persisted throughout the Holocene at the sites in eastern Russian Karelia.

ii) Climate is the main driver of long-term regional scale vegetation changes. However, at the local scale the role of climate is smaller, whereas the role of local factors increases. Furthermore, the relatively high amount of variation in long-term boreal forest composition explained by site and the relatively high amount of the variation remained unexplained by the environmental variables included in this work suggest that intrinsic site-specific factors have an important role in stand-scale dynamics in the boreal forest.

iii) In long-term perspective, when the whole 9000 year study period is considered, forest fires explain relatively little of the variation in stand-scale boreal forest composition. However, the low importance of forest fires on long-term forest composition might be attributable to the variation partitioning method. When shorter time periods are considered forest fires have a significant role in stand-scale forest dynamics. The results from wavelet coherence analysis suggest that fires can have a significant effect on the short-term changes in individual tree taxa as well as have a longer profound effect on forest structure.

iv) The results show relatively low importance of human population size on variation in long-term boreal vegetation. However, it is not suggested that the effect of human population size on long-term boreal forest composition is insignificant, but the low importance is likely due to the differences in the spatial representativeness between the human population size data and the forest composition derived from pollen data.

Although the results strongly support the importance of climate as the main driver of long-term boreal forest dynamics, it is important to note that in stand-scale forest dynamics, the effect of climate is largely modified by the local characteristics. Therefore better understanding of the processes behind the boreal forest dynamics requires investigations into different spatial and temporal scales. Disentangling the species specific interactions between environmental variables and tree species as well as the large scale dynamics of the boreal forest ecosystem provides information to predict the possible future changes in boreal forest dynamics and also provide a means to better forest management practices and the conservation of the diversity of the boreal forest.

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